Strong and weak competitors can coexist in the same niche

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Abstract

The competitive exclusion principle postulates that two trophically identical but fitness different species can not stably coexist in the same niche. However, this principle contradicts the observed nature's species richness. This fact is known as the biodiversity paradox. Here using a simple cellular automaton model we mechanistically show how two trophically identical, but fitness different species may stably coexist in the same niche. As environment is stable and any trade-offs are absent in this model, it strongly violates the competitive exclusion principle.

Keywords: white-box model, mechanistic mechanism, biodiversity, competition, conservation biology, cellular automata, biodiversity, fitness, regeneration niche, competition model, vegetative propagation

A niche is a habitat i.e. a combination of environmental factors which influence growth, survival, and reproduction of a species. Lotka-Volterra model predicts coexistence of two species in one niche when, for both species, an interspecific competition is weaker than intraspecific one. This interpretation follows directly from the Lotka-Volterra model, and no doubt about it. However, further interpretation of this interpretation, known as the competitive exclusion principle contradicts the actual species richness. The problem is that Lotka-Volterra model is phenomenological, and as a result no physical insight is available.

In this paper mechanistic mechanisms of competition are modeled on the basis of prepublished method[1-5]. We consider a competition of two species in an ecosystem consisting of three or four microhabitats (Figs 1 and 2, respectively). The closest biological analogue of the model is a competition of vegetatively propagating turf grasses. A whole ecosystem is modeled by a whole one-dimensional cellular automaton lattice. Each site of the lattice simulates a microhabitat, which in the free state contains resources for existence of one individual of any species and can be occupied by one individual only. A life cycle of an individual lasts a one iteration of the automaton. All states of the cellular automata model have the same duration. All individuals of all species consume identical quantity of identical resources by identical way i.e. they are identical per capita consumers. Each microhabitat may be in one of the five states. A microhabitat may be free (1), occupied by an individual of the first (2) or second species (3), or may be in the regeneration state after the death of an individual of the first (4) or second species (5). The death of individuals follows their life, and the regeneration of a microhabitat follows after the death of an individual. After the regeneration state a microhabitat may be occupied by a new individual or remains free. By introducing the regeneration state of a microhabitat we take into account the phenomenon of regeneration in plant communities[6,7]. Vegetative propagation occurs during an individual's life. Individuals are immobile on the lattice and populations spread only due to propagation of individuals. A rizomny sprout of the future grass tiller (horizontal creeping shoots by means of which the plants vegetatively formed during life of the parent individual) develops into an adult individual tiller after the death of the parent one. Rhizomes are horizontal creeping shoots by means of which the plants vegetatively propagate themselves. Unlike roots, rhizomes have buds, nodes, and scaly leaves. Rhizome develops tillers with roots and leaves at nodes along its length. Tiller is a minimal relatively autonomic grass shoot that sprouts from the base of grass and which is able to propagate. We define fitness as the ability of an individual to survive in a given environment and compete for its resources. The competition is carried out when various individuals are trying to use the same limiting resources (Fig. 1a). Fitness in our model is the primary ability of an individual of a species with greater fitness to occupy a free microhabitat in a direct conflict of interest with an individual of a less adapted species (Fig. 2b). The habitat is stable and the competing species have no any trade-offs. Increasing the ecosystem size by one microhabitat at the same cellular automaton rules leads to a stable coexistence of individuals of the competing species (Fig. 2). This is the simplest case of the strong violation of the competitive exclusion principle[3]. A direct supplanting of one individual by another is impossible because we exclude predator-prey interactions between individuals in the model (Fig. 2b). The violation of the competitive exclusion principle occurred due to the definite initial positioning of the individuals on the lattice, to regeneration processes in microhabitats, and to small size of the ecosystem (Fig. 2). The small size of the ecosystem does not allow to individuals of the first species to bypass individuals of second species from "flanks". The barrier of the two microhabitats in the regeneration state between individuals allows to divide the limiting resources peacefully (Fig. 2c).

Thus, on the very simple cellular-automata model we have shown a mechanistic mechanism of how strong and weak competitors can stably coexist in one niche. Our model is deterministic individual based cellular automata and is a white-box model of interspecific competition. This fact provides its mechanicalness.

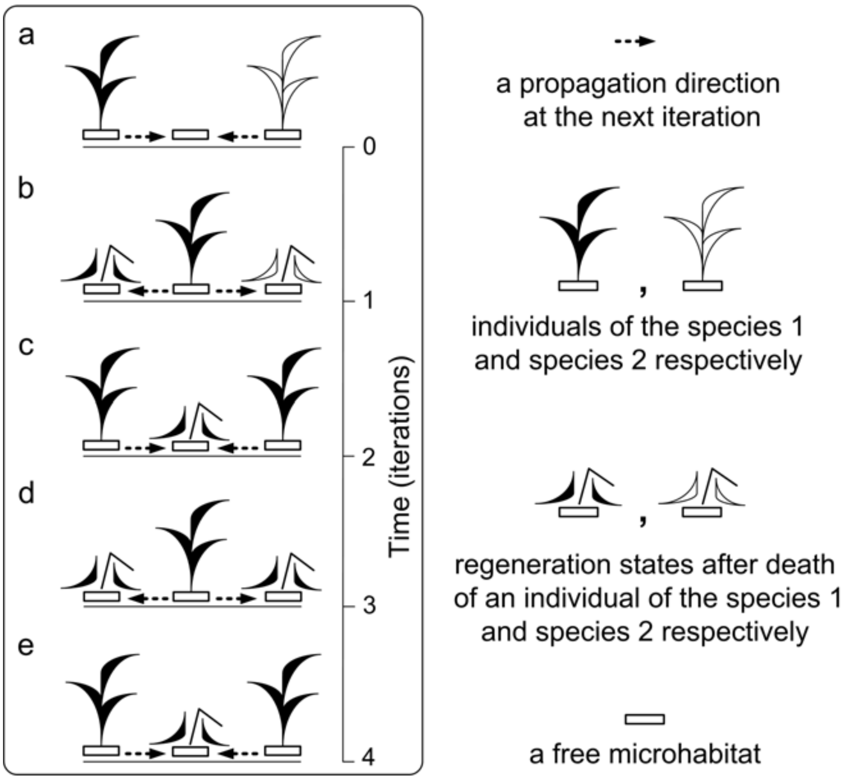

Figure 1 | Competitive exclusion of one species by another. The species 1 has greater fitness than the species 2. **a**, The conflict of interest between individuals of competing species for a microhabitat for propagation. **b**, The more adopted species wins in result of competition. Dead individuals are recycled at the regeneration state of a microhabitat. **c-e**, The first species continues to live and propagate.

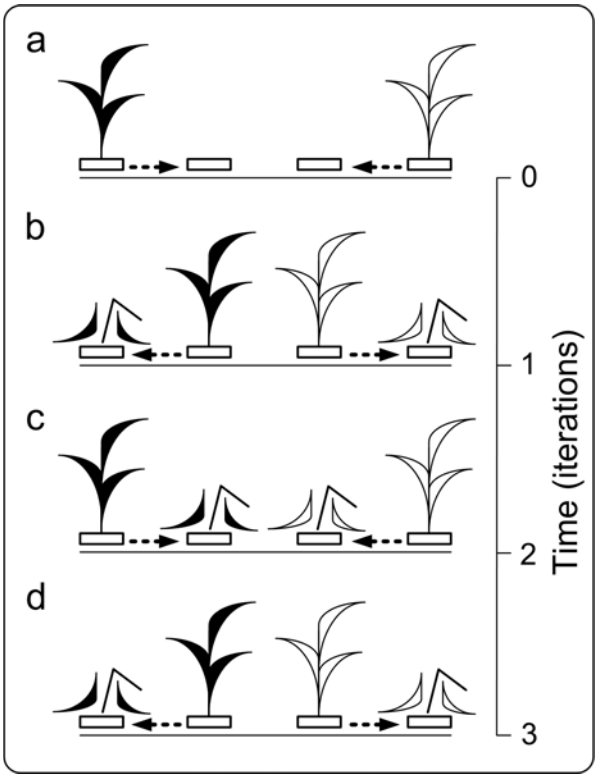

Figure 2 | Violation of the competitive exclusion principle. Stable coexistence of the competing species. **a,** Individuals propagate in the adjacent free microhabitats. Direct conflicts of interest are absent. **b,** Individuals can not directly supplant each other because they are not a predator and a prey. **c-d,** A stable cycle of coexistence of two species.

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